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Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities

Tom H. Oliver^{1*} and Mike D. Morecroft²

Global change drivers are known to interact in their effects on biodiversity, but much research to date ignores this complexity. As a consequence, there are problems in the attribution of biodiversity change to different drivers and, therefore, our ability to manage habitats and landscapes appropriately. Few studies explicitly acknowledge and account for interactive (i.e., nonadditive) effects of land use and climate change on biodiversity. One reason is that the mechanisms by which drivers interact are poorly understood. We evaluate such mechanisms, including interactions between demographic parameters, evolutionary trade-offs and synergies and threshold effects of population size and patch occupancy on population persistence. Other reasons for the lack of appropriate research are limited data availability and analytical issues in addressing interaction effects. We highlight the influence that attribution errors can have on biodiversity projections and discuss experimental designs and analytical tools suited to this challenge. Finally, we summarize the risks and opportunities provided by the existence of interaction effects. Risks include ineffective conservation management; but opportunities also arise, whereby the negative impacts of climate change on biodiversity can be reduced through appropriate land management as an adaptation measure. We hope that increasing the understanding of key mechanisms underlying interaction effects and discussing appropriate experimental and analytical designs for attribution will help researchers, policy makers, and conservation practitioners to better minimize risks and exploit opportunities provided by land use-climate change interactions. © 2014 The Authors. *WIREs Climate Change* published by John Wiley & Sons, Ltd.

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INTRODUCTION

It is widely acknowledged that global change drivers interact in their effects on biodiversity. However, most studies consider the main effects

of a single driver, or where multiple drivers are examined, the combined effects of all drivers are reported. Very few experiments and analyses are designed to investigate interactions between drivers (e.g., antagonistic interactions or synergies). Exploring interactions requires careful experimental and analytical design, which is hard to achieve at a sufficient scale. However, such interactions could potentially have large impacts on biodiversity and important implications for habitat and landscape management.

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In this review, we aim to bring together some of the key studies investigating main effects of climate and land use change on biodiversity, together with consideration of combined effects. Other drivers (e.g., invasive species) may also interact with land use and climate change to impact biodiversity,^{1,2} but we do not deal with them in this review. By 'land use' we include land cover type (e.g., arable, improved grassland, extensive grassland), and also the management of such land (e.g., cropping patterns, fertilizer inputs, grazing regimes). Other disturbance effects such as erosion and wildfires are a function of both land use and climate and are mentioned in our discussion of interactions. The review was conducted by selecting representative examples of the different mechanisms whereby climate change and land use interact to produce impacts upon biodiversity. As such, it is not an exhaustive summary of the literature in each area, but rather a selection of key examples for each mechanism. We draw upon global examples, but it should be recognized that there is a strong geographic bias in current research. So, inevitably, many examples, come from northern hemisphere temperate regions. These studies investigate how: (1) landscape structure affects species' range shifts in response to climate change, (2) climate change affects metapopulation persistence, (3) habitat and topographic heterogeneity provide microclimatic refuges, (4) the impacts of extreme climate events are influenced by land use, (5) climate-induced community shifts are influenced by land use, and (6) disturbance effects on biodiversity are mediated through land use and climate.

A second aim is to review the mechanisms by which climate and land use change can interact to affect biodiversity. In light of these complex interactions, we examine some of the problems in the attribution of biodiversity changes to climate or land use change and describe how errors can influence the accuracy of biodiversity projections. We conclude by identifying research gaps to improve our ability to attribute biodiversity changes and discuss the risks and opportunities for successful management provided by the existence of land use-climate change interaction effects.

CLIMATE CHANGE AS A DRIVER OF BIODIVERSITY CHANGE

A wide variety of studies have investigated the responses of biodiversity to past periods of climate change in the Earth's history. Biodiversity is likely to be affected by both incremental changes in mean climate parameters and also by the frequency and intensity of climate extremes.³ Although climate changes

are likely to be implicated in some mass extinction events,^{4,5} there appears to have been relatively few extinctions during the more recent glacial to interglacial transition periods of rapid climate change.⁶ Species are expected to have survived through combinations of shifting their distribution to track climate, persisting in climatic refugia and evolving tolerance to climate changes.^{6–9} However, future climate change could potentially occur at an unprecedented rate, and also against a backdrop of other drivers of change (e.g., heavily modified landscapes, pollution, eutrophication). Therefore, any generalities of extinction dynamics from ancient evidence need be contextualized within current pace of climate change and interactions between drivers need to be understood.¹

Many studies have explored effects of modern climate change on biodiversity and several major reviews have been published.^{10–13} The most well studied effects of climate change can be grouped into a number of active fields of research, which we briefly summarize in Table 1.

Each of the phenomena described in Table 1 can reasonably be expected to increase in frequency or magnitude with the extent of climate change. With no sign of respite in the rise of global CO₂ emissions, mean global temperatures, and frequency of extreme events could rise dramatically.⁴⁸ These impacts of climate change also occur in the context of global ecosystems already highly modified by land use change.

LAND USE AS A DRIVER OF BIODIVERSITY CHANGE

The major human impacts on biodiversity to date are probably through land use changes and habitat loss.^{49,50} Also, a whole range of other global change drivers are important including biological invasions, pollution (e.g., N and S deposition) and overexploitation.¹ Land use change, often to expand agriculture, causes direct habitat loss, but also has other effects such as fragmentation of remaining habitat and increased agrochemical inputs into surrounding natural (or semi-natural) habitats.^{51,52} Changes to the management of land (e.g., grazing regime) also have large direct impacts on biodiversity.⁵³ Intensification often leads to an increase in nitrogen supply, as a result of atmospheric deposition as well as direct fertilizer application. This leads to an increase in soil fertility and increased dominance of plants adapted to high-nutrient soils, which often out-compete other species.⁵⁴

Similar to climate change, species show much variation in their responses to land use change. Species benefitting from- or more tolerant to- land use change

TABLE 1 | Well Studied Direct Responses of Species to Climate Change

Response to Climate Change	Description
Phenology	Advances in the timing of biological events in spring-time in temperate regions have been documented for many groups; there is also some evidence of delayed phenology in the autumn. ^{12,14} Such changes can cause temporal mismatches between interacting species, and have the potential to lead to population declines and ultimately extinctions. ^{15–20} They also affect ecosystem processes such as productivity. ²¹
Distribution shifts	There is a large amount of evidence for expansions of species high latitude range edges towards the Earth's poles and to higher altitudes, although there is also much variation in species' responses. ^{22–26} There are considerable geographic and taxonomic biases in these studies with less data from tropical regions and the Southern hemisphere and for less charismatic groups. There is less evidence of range retractions at low latitude range boundaries, but these may be more difficult to detect; because, e.g., a grid cell of certain resolution needs to lose all individuals before a species is considered absent. ^{27,28} Ultimately, whole biomes are projected to shift, with savannahs replacing rainforest and boreal forest encroaching on tundra. ¹³ However, there is likely to be much variation in the responses of species. ^{22,29,30}
Population responses to altered weather	The abundance of many populations is strongly driven by weather variables. ^{31,32} Changes in climate are therefore projected to have large impacts on populations within their existing ranges. Seasonality is an important component of this: In the UK, some insect species may decline due to the warmer wetter winters which are projected from models. ^{32,33} Spring and summer drought events may also cause future declines in some species, while benefitting others. ³⁴
Evolutionary changes	Evolutionary changes in response to climate change are less well researched than range and phenology shifts, but there is clear evidence that in some cases selection for dispersal may increase towards range boundaries. ^{35–37} Climate change may indirectly drive selection pressures through effects on spatial structuring of populations and the availability of suitable unoccupied habitat. Effects of range expansion on the genetic structure of species are being increasingly explored (e.g., Refs 38, 39). For example, populations at expanding range margins may experience greater genetic drift and consequently lower genetic diversity. ^{39,40} There may be directional selection for certain traits such as dispersal and reproduction and trade-offs in other traits such as competitive ability. ⁴¹
Community shifts	Due to interspecific variation in responses to climate change in terms of species' phenology, their distribution and population responses to altered weather patterns, community compositions are likely to change over time. ^{42,43} For example, in the UK and northwest Europe, bird and butterfly communities are increasing dominated by species with warm-rather than cold distributions. ⁴⁴ Such community changes lead to altered interactions between species, ⁴⁵ although it is yet unclear to what degree the stability of food webs is altered by climate change. The effects of community changes on the stocks and resilience of ecosystem services is also an active field of research. ^{46,47}

tend to be more mobile, resource generalists with wider habitat associations.^{29,30}

Globally, the extent of land use change varies markedly. Some areas still have relatively pristine habitat cover (e.g., parts of tropics and the polar regions). However, in some of these areas, including many tropical areas, the pressures of increased agricultural expansion are greatest, and we can expect dramatic changes to biodiversity as a consequence of land use change.² Additionally, it has been suggested that in regions with a shorter history of human development, species may be more sensitive to land use change.⁵⁵ However, this hypothesis has not yet been tested.

In areas with a long history of landscape modification, such as NW Europe, remaining semi-natural habitats tend to be declining in species' abundance and richness, at least partly as a consequence of fragmentation.⁵⁶ Isolated populations face increased extinction risk and metapopulations (groups of connected populations) need a minimum number of sites occupied to persist.⁵⁷ Isolation effects may be nonlinear, with greatest risks to populations when total habitat area is low.^{58,59}

It is possible that conversion of land to intensive agriculture in NW Europe may have now peaked, with increased emphasis on restoring semi-natural habitat cover (e.g., managed through agri-environment

schemes). For example, according to the Countryside Survey, across the UK between 1990 and 2007 there was a 9.1% decrease in arable and horticulture land cover, but also a concurrent increase in improved grassland of 5.4%.⁵⁴ However, predicting future trends is difficult as suitable high resolution land use change scenarios are lacking.^{60,61} Predicting complex socioeconomic systems is very difficult. Across Europe, e.g., Common Agricultural Policy reform is likely to have impacts on land use patterns, as are increased human population size, changes to urban planning policies and effects of climate change on agriculture.

At a broad global scale, conversion of land to agriculture to meet growing food demands is set to continue.^{62,63} Unchecked, this will continue to have severe negative impacts on biodiversity.

COMBINED EFFECTS OF CLIMATE AND LAND USE CHANGE ON BIODIVERSITY

Understanding interactions between global change drivers will be essential to manage environments appropriately in the face of future changes.^{1,2,45} An increasing number of studies have begun to examine these combined effects on biodiversity, although studies exploring true interaction effects are less common. Ultimately, we need to tease apart the complexity caused by interactions between drivers.

Mantyka-Pringle et al.⁶⁴ collated 1319 studies on the effects of habitat loss from around the globe and conducted a meta-analysis on interactions between habitat loss effects and climate. They found that the effects of habitat loss were greatest in areas with higher mean temperatures and where mean precipitation had decreased over time. This led to the conclusion that 'management strategies should focus towards areas with warmer climates, especially those that are more susceptible to precipitation change'. However, such a conclusion may be premature, because of the limited nature of the input data to this analysis. The effects of habitat loss on biodiversity were simply scored as a binomial variable (negative vs non-negative), potentially missing important quantitative effects. More importantly, however, the degree of habitat loss itself was not included in the analysis, presumably because data were not available. Therefore, the authors could not control for confounding correlations between habitat loss and climate variables (they did test for correlations between total habitat area and climate, but habitat area and habitat loss are not the same). For example, the extent of habitat loss could be far greater in the tropics, leading to the erroneous conclusion that

effects on biodiversity are due to interactions with climate, when they are really due to direct effects from greater habitat loss, reflecting increasing human populations, and a variety of socioeconomic factors.

Nevertheless, such studies attempting to understand the combined effects of land use change and climate change across space are a step in the right direction. We would expect global differences in the magnitude of these individual drivers. Land use change is expected to continue to be a major driver in the tropics, while the magnitude of temperature change is expected to be greatest towards the poles.^{65,66} In addition the impact of any given temperature rise will differ between species and between ecosystems and may cross critical thresholds in some places (e.g., changes in biotope at upper elevation tree lines) but not others. Within countries, there may be regional differences in the intensity of land use and climate change. For example, in the UK, high intensity arable agriculture tends to occur more in the south and east, while projections of changes in temperature and rainfall also vary regionally.^{33,67} In Catalonia, Stefanescu et al.⁶⁸ found that increasing aridity and land use intensification are primarily responsible for declines in generalist butterfly species in lowland regions, while climate warming and land abandonment have caused serious declines in specialist species in mountain areas.

These spatial patterns in land use and climate change cause spatial patterns in the impact on species. For example, species richness of Californian butterflies has declined at lower elevations where land use is more intensive. This direct effect reduces the pool of species available to colonize higher elevations and exploit new opportunities provided by climate warming.⁵⁵ In the UK, a qualitative analysis of several species indicated that projected impacts of climate change on species' varies regionally and that the most appropriate adaptation actions also depend on local variation in the quality, area, and configuration of key habitats.⁶⁹ Studies such as these highlight the difficulties in teasing apart the quantitative effects of land use and climate change. Nevertheless, it is possible to qualitatively distinguish a number of ways in which climate and land use change interact to affect biodiversity. The most well established types of interaction are described below:

Landscape Structure Affects Species Range Shifts

The most well studied interaction is the impact of land use on species' ability to shift their distributions in response to climate warming.^{70,71} Intensively managed landscapes may severely hinder the movement of

species and their ability to cope with climate change through tracking of climate envelopes.^{7,72} Not all species are equally affected, with mobile generalists more able to disperse and establish new populations within human modified landscapes.^{22,29,30} This follows the general pattern, whereby species most able to persist in the face of synergistic global change drivers have larger geographical ranges and greater dispersal ability.¹

Climate Change Affects Metapopulation

Persistence

Direct impacts from climate change on species' local population sizes can also alter their ability to cope with habitat fragmentation.^{59,73} If climate change depresses mean population sizes or causes increased stochasticity in population dynamics, e.g., as a consequence of increased incidence of extreme events, then habitat networks may require larger patches to maintain metapopulations.⁷³ Connectivity between habitats may also need to be improved.⁷⁴ For some species, climate warming may have positive effects on dispersal, effectively increasing functional connectivity between populations.⁷⁵

Habitat and Topographic Heterogeneity Provide Broader Microclimatic Gradients

The climate experienced by species on a local scale is often a key determinant of population growth, and fundamental niche space (*sensu* Ref 76) Microclimates can differ markedly between different topographies and habitat types.^{77,78} An extreme example is that of forest cover which substantially reduces solar radiation at the soil surface and also lowers the temperature compared to open sites on sunny days. There is also a buffering effect in that, while surface temperature is cooler at midday, it is warmer at night compared to grasslands.^{79,80} Soil type and structure can also influence microclimate by affecting moisture retention.⁸¹ There is an interaction with landscape characteristics, particularly patch size, in that small patches may have different microclimates and soil conditions to large ones. The microclimate of the forest edge is very different to that of the interior with higher light levels but also drier soil conditions for tens of meters into the forest,⁸² which has demonstrable impacts on soil biodiversity and ecosystem processes.⁸³

Because of the strong influence of microtopography, soil, and vegetation type, microclimate may only be weakly correlated with macroclimate.^{84,85} Indeed, within site variation in accumulated temperatures can be as high as expected from a 300-m change in altitude or a climate change scenario corresponding to warming of 1.6–3.8°C.⁸⁴

While too small a patch size, may create problems for some species in terms of minimum patch requirements, a broad range of microclimates in a local vicinity, between which mobile organisms can move, can allow them to maintain themselves closer to their optimum environmental conditions, i.e., growth rates may be higher and populations are buffered from extreme events.^{86–89} This offers the opportunity to manage land to provide a range of microclimates and promote more resilient populations.⁹⁰ There is evidence that heterogeneity in habitat types and topographies promote more stable population dynamics of some butterfly species.⁹¹ Indeed, future microclimatic conditions may be affected as much by land use change as by climate change.⁹² Of course, the converse also applies, and homogenous land use with limited microclimatic variation (e.g., due to reduced soil and habitat diversity and flatter topography) may suffer greater impacts of climate change.^{93–96}

Nutrient Deposition Alters Microclimates

Increased nutrient deposition as a consequence of land use can alter soil fertility and increase plant growth rates.⁵⁴ It has been suggested that increased vegetative growth resulting from a combination of nutrient deposition and climate warming can cause increased shading and lead to cooler microclimates at soil surfaces.⁹⁷ Such a hypothesis could possibly explain the contraction in habitat breadths of UK butterfly species that require open, short turf habitat types, contrary to the expectation that climate warming should have increased the number of suitable microsites for these species.⁹⁸ However, such evidence provides only tentative support of this hypothesis and further analysis and experimentation is necessary; but a potential causal pathway does exist, whereby land use affects plant growth, which will in turn alter surface microclimate and influence species' responses to changes in macroclimatic conditions.

Impacts of Extreme Climate Events Are Influenced by Land Use

Population responses to extreme climate events, such as drought, are likely to be affected by habitat quality, area, configuration and heterogeneity.⁹⁹ Therefore, some authors have raised the need to consider the impacts of drought in the context of other drivers of environmental change, such as land use.¹⁰⁰ Such research is beginning to accumulate. For example, habitat fragmentation can impact the sensitivity and recovery of insect populations to drought events.^{101–103}

Climate-induced Community Shifts Are Influenced by Land Use

Through all the mechanisms described above, land use can influence changes in community structure under climate change.⁴² It has been observed that extreme climate events, such as intense prolonged drought, can have drastic effects on the structure of communities,^{34,100,104,105} and it is likely that such effects are mediated by land use.¹⁰⁶ There is also evidence that land use-related variables can interact with rising CO₂ concentrations. For example, responses of decomposer communities to CO₂ enrichment vary depending on N deposition.^{107,108} Similarly, the colonization of plants by arbuscular mycorrhizal fungi declines with N deposition, but can increase with elevated CO₂.^{109,110}

Multiple interacting global change drivers produce complex effects on communities, but from a synthesis of 688 studies Tylianakis et al.⁴⁵ manage to draw a number of generalizations, including negative effects on mutualisms involving plants, context-dependent multitrophic responses of soil food webs and altered dominance of plant and animal species.

Natural Disturbance Regimes Are Affected by Both Land Use and Climate Change

Natural disturbance regimes such as erosion, flooding, and wildfires are all affected by anthropogenic land use. For example, deforestation reduces soil stability leading to increased soil erosion rates¹¹¹; flood risk is affected by canalisation of natural river courses¹¹² and land management of coastal zones¹¹³; wildfire frequency is affected by changing land use.^{114,115} All these processes are also likely to be impacted by climate change leading to interactive effects. For example, changes to the total amount and the timing of precipitation will affect erosion rates¹¹⁶; flood frequency is expected to increase under sea level rise and increased storm surges⁶⁵; wildfire frequency may be increased under increased aridity as a consequence of climate change.^{115,117}

There are therefore a number of phenomena in which the combined effects of land use change and climate change have been shown to impact biodiversity. Interspecific variation in responses to combined effects of land use change and climate change appears to be common, as it is with the direct main effects of these drivers.^{118,119} For some species and communities, interacting effects have the potential for large negative impacts; land use change can reduce resilience to climate change and, conversely, climate change can hinder the ability of species to cope with modified land use. Therefore,

there is an immediate need to better understand these interactions.^{1,2} In particular, many studies do not adequately control for the effects of one driver while assessing another, meaning that the importance of interactions (versus additive effects) cannot be assessed. To better investigate these effects, we below provide a review of possible interaction mechanisms to aid researchers in experiment and analysis design.

MECHANISMS UNDERLYING CLIMATE–LAND USE INTERACTIONS

An interaction occurs when two explanatory variables have an effect upon a response variable that is greater (synergism) or lesser (antagonism) than the effects expected from the explanatory variables acting independently, i.e., effects are ‘multiplicative,’ rather than ‘additive’ (Figure 1).

Didham et al.¹²⁰ in a review of interactions between habitat loss and invasive species, suggest that interaction effects can be ‘chain effects’ or ‘modification effects’ (Figure 2; adapted from Ref 120). Interaction chain effects occur when one driver (e.g., habitat loss) increases the magnitude of another driver (e.g., abundance of invasive species) and both drivers have a direct effect on the response variable. In contrast, interaction modification effects occur when the per capita effect of one driver (e.g., the negative effect of a single individual of an invasive species) changes depending on the level of another driver.

With regard to land use and climate change, direct interactions between these drivers are expected. Land use patterns across the globe will affect climates by altering the balance of carbon in terrestrial and atmospheric pools.^{121,122} In addition, land use can affect regional climate because different land cover types have different impacts on surface fluxes of radiation, heat, moisture and momentum.¹²³

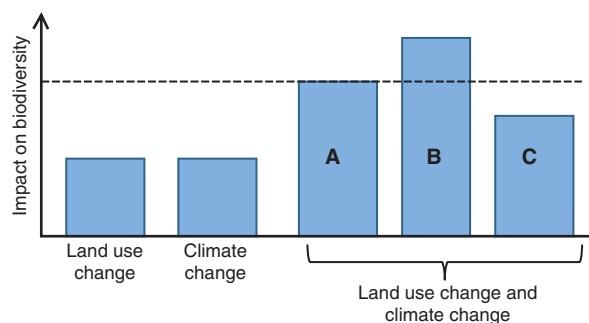


FIGURE 1 | Combined effects of land use change and climate change on biodiversity. Effects may be additive (column A), synergistic interactions (column B), or antagonistic interactions (column C).

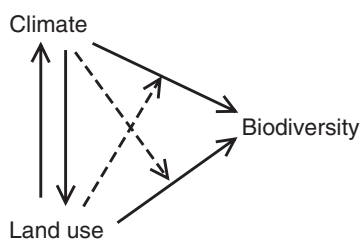


FIGURE 2 | Interactive effects between climate change and land use on biodiversity. Interactions may arise through chain effects, whereby one driver increases the magnitude of another driver (solid arrows), or through modification effects, whereby the per unit impact of one driver on biodiversity is contingent on levels of the other driver (dashed arrows). (Reprinted with permission from Ref 120. Copyright 2007 Elsevier)

Conversely, climate change can also influence land cover and land use.¹²⁴ Firstly, climate will directly influence the climax vegetation type expected in any given region, e.g., tropical rainforest, savannah, boreal forest, etc.¹²¹ In addition, climate change will also affect land use through changes to socioeconomic systems and policy responses.¹²⁵ For example, the UN REDD + program aims to reduce deforestation and enhance forest carbon stocks and conserve biodiversity (<http://www.un-redd.org/> accessed March 23, 2012). Agricultural practices may also be adapted to the changing climate, e.g., through the use of different crop types such as sunflowers and maize grown further north in Europe and North America, or altering the timing of sowing and harvesting. In addition, regional droughts may lead to increased irrigation of arable agriculture, altering water available for wider biodiversity. All these impacts of climate on land use, and land use on climate, may have large effects on biodiversity.

Impacts of the interaction chain effects on biodiversity described above can be predicted by monitoring climate and land use change and by understanding their direct effects on biodiversity. However, in addition to these interaction chain effects, modification effects are likely to occur, where the per unit impact of climate change (e.g., per degree of temperature rise) on biodiversity is contingent on land use (e.g., levels of pollution). Similarly, the per unit impact of land use change (e.g., per hectare of habitat converted to agriculture) on biodiversity may be contingent on climate change. In this review, we focus mainly on interaction modification effects because they are less well studied than direct effects and may lead to unexpected, potentially large negative impacts on biodiversity. Below we describe a number of mechanisms by which these interaction modification effects may occur.

Interactions Between Demographic Parameters

Both climate change and land use can affect a number of demographic parameters and there may be interactive effects. For example, edge effects may cause habitat dessiccation and increased species mortality, which is exacerbated under extreme weather conditions.^{82,126} More examples are listed in Table 2. In many cases, demographic effects may be additionally mediated through altered competition between species. For example, a changing climate may push a plant species closer to the edge of its fundamental niche space, reducing its competitive ability and allowing other plant species to become dominant (limiting it to ‘realized’ niche space⁷⁶).

Evolutionary Trade-offs and Synergies

Land use and climate change both impose selection on populations for more tolerant genotypes. The tolerance to different environmental drivers may be correlated or uncorrelated.¹³⁵ Positive correlations mean that adaptation to one driver also confers tolerance to another driver. For example, the evolution of wider environmental tolerance to spatial environmental heterogeneity may improve resilience to climate change.¹³⁶ However, this also means that increasing the homogeneity of the abiotic and biotic context, as has occurred in highly modified temperate landscapes over recent decades, may reduce the ability of species to cope with climate change.^{137,138}

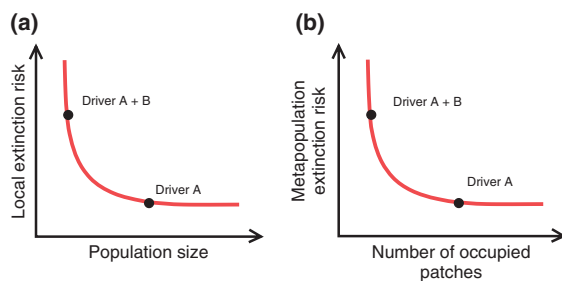
Conversely, the tolerance to different drivers may be uncorrelated or negatively correlated. If negatively correlated, then genetic variation eroded by selection from one driver will reduce the capacity to adapt to the other.^{139,140} For example, in a microcosm experiment Mora et al.¹²⁷ found that population declines caused by reduced immigration and environmental warming were up to 36 times worse when these drivers occurred simultaneously. They speculated the smaller population sizes from reduced immigration may have impaired the ability of populations to adapt to warming. However, an alternative hypothesis would be that tolerance to environmental warming is negatively correlated with fecundity or development time.¹⁴¹

Threshold Effects of Population Size on Extinction Risk

Even if the combined effects of land use and climate change on demographic parameters are additive, there may still be interactive effects on other population parameters such as extinction risk. All demographic

TABLE 2 | Examples of How Climate Change and Land Use Change Can Have Both Main and Interactive Effects on a Range of Demographic Parameters

Demographic Parameter	Climate Change Main Effect	Land Use Change Main Effect	Interaction Between Land Use Change and Climate Change
Birth rates	Temperature-dependent fecundity. ^{73,127}	Resource levels affect fecundity ¹²⁸	Fecundity depends on both temperature and the presence of conspecifics, which are both influenced by land use and climate ^{129,130}
Death rates	Temperature determines species' fundamental niche space and influences mortality ¹³¹	Edge effects can increase predation risk ¹³² ; Density-dependent mortality is determined by resource levels, which are influenced by habitat amount and quality. ¹²⁸	Edge effects may cause desiccation and increased mortality, which is exacerbated under extreme weather conditions ⁸² ; Increased pathogen infection in plants under increased temperature and nitrogen deposition. ⁴⁵
Immigration/Emigration	Temperature-dependent dispersal. ⁷⁵	Matrix structure affects immigration rates. ¹³³ Boundary types affect emigration rates. ¹³⁴	Temperature-dependent dispersal affects functional connectivity across landscapes which are also affected by land use change. ⁷⁵ Climate affects fruiting phenology and the probability of successful seed dispersal by mutualists. ⁴⁵

**FIGURE 3** | Nonlinear effects between local population size and extinction risk (a) and patch occupancy and metapopulation persistence (b) can lead to interactive effects of global change drivers on extinction risk.

parameters have the potential to influence equilibrium population size,¹⁴² and there may be nonlinear relationships between local population size and extinction risk. In particular, small populations may suffer greater risk of extinction due to genetic drift, inbreeding depression, inability to find mates and increased susceptibility to environmental and demographic stochasticity.^{143,144} Therefore, additive effects of land use and climate change drivers on population size may result in multiplicative effects on extinction risk (Figure 3(a)).

Threshold Occupancy for Metapopulation Persistence

Some species exist in metapopulations or patchy populations, whereby local extinctions of sub-populations

may occur relatively frequently, but these are recolonized through dispersal from occupied patches. Both land use change and climate change can lead to local extinction events.

Theory has shown that when the proportion of patches falls below a threshold level, the extinction of the entire metapopulation can rapidly follow.^{145,146} Therefore, even if the effects of land use and climate change are additive for any individual population, the total combined effects may lead to multiplicative effects on metapopulation extinction risk (Figure 3(b)).

All the above mechanisms might contribute to the combined effects of climate and land use change on biodiversity described earlier. For example, in the case of climate change causing species' range changes, land use causes a modification interaction effect (meaning that the effect of climate change on degree of species' range shift depends on land use in intervening regions⁷¹). The mechanisms underlying this may be due to demographics (i.e., growth and death rates vary between land use types and also with climate.¹²⁸), evolutionary effects (i.e., selection for dispersal and fecundity dependent on habitat structure^{35,147}), threshold effects of population size (i.e., smaller, low quality habitat patches with smaller populations have higher extinction risk^{143,144}) and threshold effects of metapopulation persistence (i.e., populations in fragmented landscapes have higher metapopulation extinction risk.^{145,146}

ADDRESSING ATTRIBUTION PROBLEMS

How Do We Know that Climate Change Has Caused All the Changes that Are Attributed to It?

In order to usefully inform conservation and climate policy, it is essential that we can reasonably attribute changes in populations and communities to climate and/or land use change. In order to do this, well designed experiments and analyses are required, which control for one driver while exploring the effects of another. A basic requirement is to have measurements of the degree to which land use and local climate has changed in any area, concurrent with measurements of biodiversity change. Sufficient independent samples are needed to allow statistical analyses which give an appropriate degree of confidence in associations. In these analyses, it is important that spatial autocorrelation is accounted for, to prevent anticonservative estimates of the significance of associations ('psuedoreplication').¹⁴⁸ If these conditions are met, then researchers can potentially ascertain whether changes in biodiversity across a number of sites are primarily due to climate or land use change, including quantification of uncertainty in any conclusions. However, if land use change and climate change measures are strongly correlated in space or time then regression techniques will not be able to reliably test causation.

In some cases, clear significant effects of either land use change or climate change may be identified. However, in other cases it may be difficult to separate out effects of land use and climate change. For example, in the UK, butterfly communities have changed over the last three decades, probably as a result of both drivers.^{29,149,150} Franco et al.²⁷ attempted to partition variation in population persistence of northern butterfly species to habitat loss or climate. Extinctions were attributed to habitat loss if a host plant was not found to be present in a 1-km square where a butterfly was previously found but not found upon resurvey (for one person hour). This highlights the difficulty of assessing habitat change at such large scales where host plants and butterflies might be missed. Such issues reduce the statistical power to detect effects. Nonetheless, Franco et al. did find evidence that up to 28.2% of extinctions were in areas where habitat loss was inferred (for the species *Coenonympha tullia*), and host plant occupancy was a significant predictor of extinction for this species. For the other three northern butterfly species climate-related variables (elevation, latitude and change in modeled climatic suitability) were

important predictors. These results suggest that both climate warming and habitat loss are drivers of local extinctions in these butterfly species.²⁷ However, the coarseness of the data make any quantitative partitioning of the relative importance of these drivers difficult. In addition, as this review describes, in many cases there may be strong interactions between the effects of climate and land use upon biodiversity which can complicate inference. Therefore, in order to successfully attribute effects, interactions need to be explicitly considered in experimental and analytical designs.

Investigating Interactions

Microcosm experiments can be good ways of studying interactions at a mechanistic level, allowing sufficient replication and with influences beyond the variables of interest kept constant.¹²⁷ However, their transferability to real-world situations (e.g., other species and real landscapes) may be limited.¹⁵¹ Field experiments at the plot scale are more realistic and can identify effects of climate variables with some confidence (e.g., Ref 152); a small number have also looked at interactions with management (e.g., Ref 153). However, experiments at landscape scale are not likely to be possible, due to the practicalities of manipulating land use and climate across sufficient areas and achieving sufficient replication.

One of the most efficient approaches may be to exploit natural gradients in climate and land use and use long term ecological monitoring schemes to assess effects on populations and communities. With sufficient spatial replication, climate patterns across space can be used as a surrogate for temporal patterns, and replicated across different land use classes. However, extrapolating from spatial patterns to temporal predictions can be error prone if the response variable has not achieved an equilibrium state, e.g., metapopulations may be in 'extinction debt' where the negative impacts of habitat fragmentation show a time-lag.¹⁵⁴ Alternatively, if populations are locally adapted to their environment, then space-for-time substitutions may produce erroneous conclusions.^{155–157}

Errors in space-for-time substitutions can also arise if the correlation between explanatory variables and response is not directly causal but driven by some other confounding factor.¹⁵⁸ For example, Canadian butterfly assemblages are more species rich in areas of high human population density. Taking this association as directly causal, one would predict that increasing human populations density should increase species richness. However, the opposite is, in fact, true. The spatial association between human population density and butterfly species richness is

likely to be driven by the co-variation of both these factors with other factors such as climate¹⁵⁸ and soil fertility and ecosystem productivity.

Conversely, attributing biodiversity changes to climate can sometimes be confounded by land use. For example, the community temperature index (CTI) is an increasingly used metric of the balance of cold- and warm-associated species in a given location. Under incremental climate warming, the replacement of cold-associated species in communities with more warm adapted species is expected, leading to an increase in CTI scores. Across Europe, both bird and butterfly assemblages show this general pattern.⁴⁴ These community changes are generally attributed to climate change, and CTI has been suggested as an indicator of the biodiversity responses to climate change.¹⁵⁹ However, it has been suggested that land use change may be partly responsible for changes in CTI, due to correlations between species' habitat associations and the degree to which they are classed as cold- or warm-associated. In particular, due to a latitudinal gradient in woodland cover in Europe, cold-associated species are more likely to be woodland species. Therefore, a loss of woodland may negatively impact these species and reduce CTI scores.¹⁶⁰ Therefore, Clavero et al.¹⁶⁰ suggest that land use change needs to be controlled for in assessing the effects of climate change on community composition; e.g., by stratifying analyses by land use change.

These examples illustrate the difficulty in attributing changes in biodiversity to either land use change or climate change. Analyses need to be appropriately designed with adequate spatiotemporal data on both drivers. For example, a recent study by Eglington and Pearce-Higgins³¹ compares the relative impact of climate change (temperature and rainfall) versus land use change (degree of agricultural intensification) on bird populations. Results suggest that land use change has been a more significant driver of bird declines compared with climate change to date. Although, their model did not consider interaction effects between climate and land use, these could potentially be included in the analytical framework.

Finally, where empirical analysis is not feasible (e.g., due to spatial extent of a study) then process-based theoretical modeling may play a useful role in exploring land use change climate change interactions (e.g., Refs 70, 161). However, they must be based on realistic parameters and ideally validated with independent empirical data in order to usefully inform us on outcomes of real-world interacting processes.

Influences on Projections of Changes in Populations and Communities

Understanding relationships between biodiversity and drivers of change will facilitate the assessment of the impacts of land use decisions. However, current projections for biodiversity variables rarely incorporate multiple drivers or interactions.^{2,127} Interactions may be relatively unimportant where the effects of a single driver are very great.¹ However, it is probably more often the case than multiple drivers act together to impact biodiversity.^{45,68}

Some sources suggest that climate change will overtake habitat loss as the greatest driver of biodiversity decline.^{49,61} However, others suggest that land use change will continue to be the most significant pressure.^{31,66,162} This discrepancy may partly depend on the species group and region being studied.¹³⁶ Impacts of climate change will vary between and within countries, as will land use change.⁶⁵ Some researchers have suggested that greater future land use will occur in the tropics.^{2,66} Others have suggested that regions at mid-latitude, such as Mediterranean grasslands, will experience both significant land use and climate changes; therefore, we might expect the effect of land use-climate interactions to be most apparent in these regions.²

In addition to spatial variation in land use and climate change within any region, species will also differ in their sensitivity to these drivers. For example, where species are closer to climatically determined range boundaries they are likely to be more sensitive to the effects of climate change and, consequently, any interactions between land use and climate change.^{2,89,163}

Most predictive models of biodiversity change currently simply consider one driver or combined effects of multiple drivers in very crude ways. For example, an analysis by Jetz et al.⁶⁶ classified land cover for each global 0.5° grid cell as changing either due to human land use *or* due to climate change, with subsequent effects on biodiversity proportional to the amount of original habitat cover lost. A study by Thomas et al.⁷² considering species' extinction risks from climate change used bioclimate models to estimate future areas of climatic suitability, exploring the upper and lower boundaries of species' ability to reach them by assuming infinite or zero dispersal. Hof et al.¹⁶⁴ used bioclimate models to compare spatial overlap in projected extinctions from climate change, projected land use changes and the incidence of chytrid fungus. Such frameworks may be useful for considering the combined (additive) effects between land use and climate change, but are clearly not appropriate to investigate interaction effects.

Some predictive models, however, are beginning to take into account interaction effects. For example bioclimate envelope models are being integrated with demographic models to understand how species range shifts occur in the context of altered landscape structures.^{165,166} For example, a model by Carroll¹⁶⁷ suggests that logging and climate change have interactive effects on martens in Canada and the USA. As a consequence of the dependency of species range shifts on both land use and climate change, an increasing number of studies are considering how reserve networks might be designed to promote more resilient populations.^{73,168–170} However, such models would benefit from better data on species movement¹⁷¹ and finer resolution climate and land use data, in order to better identify topographic and habitat refugia.¹⁷² Also, most models assume static land cover. To incorporate land use change, however, will require better scenarios of land use change. Coarse resolution land use scenarios do exist,⁶⁶ but projections of land use at local scales are difficult to achieve due to the large uncertainties in future land use policy and possible unforeseen changes, e.g., in world food markets. Given that decisions about land use and management are open to influence by the results of research, it may be better to approach the issue through a sensitivity analysis—determining the effects of different strategies for land use and management.

Predictive models for other land use-climate interactions, beyond species range shifts, are far less common. The effects of these interactions first need to be better quantified. For example, only when we better understand how land use moderates species responses to drought events, will we be in a position to predict how community structures might change in different regions under climate change.¹⁰¹

To reduce uncertainty in future projections, research on the synergistic effects of multiple global change drivers needs to continue.^{2,13} Both climate and land use change will also interact with other drivers. For example, climate change may increase probability of biological invasions^{42,120} and disease susceptibility.¹⁷³ In addition, the ability of populations to cope with these drivers through rapid evolution needs more investigation.^{174,175} For example, local adaptation to climate conditions and land use patterns are likely to affect species responses to these threats.^{38,157,176} To address this question, transplant experiments could be conducted, or genetic data could be collected across species ranges and analyzed together with population data from long term spatially replicated monitoring schemes.

RISKS AND OPPORTUNITIES

Interactions between climate change and land use change present a number of risks for biodiversity conservation, but also several opportunities. The complex nature of interactions between global change drivers means that we may never have accurate predictive models for biodiversity impacts. For example, the effects of increased drought under climate change may be moderated by local land use, but climate change also affects species phenology which will influence their sensitivity depending on when in the year a drought occurs. In addition to interaction chain and modification effects between drivers, the effects on individual species may cascade through communities causing unanticipated effects.¹ These problems are in addition to the fact that there are clear difficulties in obtaining reliable projections of land use and climate change on which to base our projections for biodiversity. Therefore, predicting combined effects of multiple drivers on biodiversity is particularly challenging.⁹

Despite this uncertainty in future trends of climate and land use change and in species responses to these interacting drivers, it is important to attempt to understand these effects, otherwise current conservation practice may become ineffective. Inappropriate habitat management could exacerbate biodiversity declines. For example, in temperate regions under a warmer climate, prescriptions for scrub clearance on sites vulnerable to high soil moisture deficit may reduce the availability of cooler moister microclimatic refuges which will allow species to persist. At a larger scale, the location of protected areas may need to be re-assessed in light of shifts in species ranges and sea level rises.¹⁷⁷ For example, populations of shore birds may start to use different geographical locations around a coastline and protected areas may need to move with them; although caution is required as evidence is emerging that new species may preferentially colonize existing protected areas.¹⁷⁸ In addition, suitable conditions may not be easy to create in new areas. For example, the past history of land management may be critical in maintaining low nutrient conditions or other habitat characteristics (e.g., old trees) which allow a wide range of species to persist.^{179,180}

From a more positive perspective, interactions between land use change and climate change present opportunities to lessen climate change impacts by adapting land use and management. Adaptation to climate change has become a major priority for conservation, it can be defined as '*adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm*

or exploits beneficial opportunities' (IPCC 4th Assessment report Working Group 2 Glossary <http://www.ipcc.ch/pdf/glossary/ar4-wg2.pdf>). A wide range of high level principles for adaptation have been identified.^{74,181} Climate change adaptation can be viewed as a spectrum of responses from building resilience of existing ecosystems, populations, and communities to accommodating inevitable change, to promoting transformational change.¹⁸²

Building resilience has different aspects at different scales.¹⁸² At the level of the individual habitat patch, it may be possible to directly manipulate the microclimate experienced by species by changing management. For example in a grassland surface temperature at ground level can be lowered by allowing the sward to grow taller or allowing the growth of areas of scrub. Recent research suggests that optimum turf height for conservation of *Maculinea* butterflies is changing with increasing mean temperatures.¹⁸³ Management intervention can also help to maintain a species where it is at risk of increased competition from other species (whether invasive or already present).

At the landscape scale, increasing the size or number of patches may increase the resilience of communities and populations by increasing the effective size of populations and reducing edge effects.^{69,184,185} This is particularly important in landscapes that are intensively managed in which natural or semi-natural habitats are highly fragmented. In many cases, it will not be possible to quickly restore natural vegetation types, but there may be a beneficial effect of buffering core areas of an ecological network with areas that are being restored. Within a European context, funding for agri-environment measures under the Common Agricultural Policy represent a major opportunity for this with appropriate targeting. This approach can also facilitate dispersal between habitat patches, increasing the functional connectivity of networks of sites and enabling metapopulation function.^{186–188}

In some systems, ensuring that the physical environment allows ecosystem function to be maintained is the priority for adaptation. This is particularly true in wetland systems: maintaining the water supply is essential for function and support of species. The effects of rising temperatures and possible droughts can be offset by a range of approaches, including blocking drainage channels and reducing abstraction for other purposes such as agriculture. In practice this requires a joined up approach to land management in which the needs of conservation and other land uses are balanced. So, maintaining some fresh water and wetland systems in a changing climate

may be best achieved by improving water use efficiency in agriculture and managing catchments to retain water more effectively. This might include engineering solutions such as farm reservoirs; however, there is increasing interest in ecosystem based adaptation where managing the natural environment provides benefits for both people and biodiversity. Restoring wetlands and strategically creating them within flood plains, together with reduced canalisation of rivers can help to ensure water is retained longer in wetlands and slowly released, maintaining water supply and reducing flood risks for people.

The complexity and unpredictability of the interactions between climate change and land use mean projections are best viewed as a range of plausible futures to guide the development of adaptation measures. Adaptation is likely to be most effective when it adopts a 'no regrets' approach and uses actions that are relevant to a range of scenarios. Adaptation also needs to proceed using an adaptive management approach, where management can be adjusted on the basis of experience and unanticipated effects can be addressed.^{189,190} To achieve this, spatially replicated long term biodiversity monitoring schemes are essential. Such monitoring should aim for good coverage across land use and climate gradients and be integrated with meteorological monitoring and the recording of land use and management. Current monitoring is often spatially, temporally and taxonomically biased.⁵⁰ In the UK, for example less monitoring occurs in more sparsely populated areas of Scotland and Wales and there is less monitoring of species which are not charismatic, but which nonetheless may have important functional roles in ecosystems.¹⁹¹

Although the complexity of interactions between global change drivers can be daunting, it is reassuring the relatively simple actions may reduce the impacts of a number of drivers simultaneously. For example, increasing habitat quality or area (e.g., by creating or restoring habitat adjacent to occupied patches) can reduce the impact of edge effects and increase population sizes, making populations less susceptible to extinctions induced by environmental and demographic stochasticity. Simultaneously, these actions also increase functional connectivity of populations (by increasing propagule pressure and colonization probability;¹⁸⁴) and increase the genetic variation within populations, giving them greater capacity to evolve tolerance to environmental drivers.¹²⁷

CONCLUSION

Climate change and land use change interact to impact biodiversity through a wide range of mechanisms.

Understanding these interactions will be necessary to more reliably project changes in biodiversity under different land use and climate scenarios and to manage habitats appropriately. There are also opportunities to reduce the negative impact of climate change on biodiversity through adaptation strategies (e.g., Ref 192), and relatively simple actions such as increasing habitat quality and extent can simultaneously address multiple drivers. However, land use decisions can also have negative impacts on the 'adaptive capacity' of populations.¹⁹³ Land use is driven by socioeconomic and climatic factors, potentially with complex

feedbacks; but if we cannot suitably address the negative impacts of land use change, then we close off our options for dealing with climate change.¹⁸⁸ With a growing recognition of the existence of interactions between global change drivers, conservation strategies and biodiversity projections that only address a single driver are inadequate. Future research needs to understand and quantify the major mechanisms by which global change drivers interact, in order to minimize risks and increase opportunities for the conservation of biodiversity.

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